THE VALIDITY OF *MALACORAJA* STEHMANN, 1970 (CHONDRICHTHYES, BATOIDEI, RAJIDAE) AND ITS PHYLOGENETIC SIGNIFICANCE

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(With 5 figures and 1 table)

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ABSTRACT

The clasper structure, neurocranial form and proportional dimensions of the first adult male of *Raja spinacidermis* Barnard, 1923 are described. On the evidence presented the recognition of the subgenus *Malacoraja* Stehmann, 1970 is substantiated. *Malacoraja* appears to be the linking subgenus between *Breviraja* and rajids of the *Dipturus*/*Rajella*/*Amblyraja*/*Leucoraja*-line of evolution.

CONTENTS

INTRODUCTION

During the course of investigations on the systematics of the Rajidae of the eastern North Atlantic, Stehmann (1970) defined a new monotypic subgenus, *Malacoraja*, for *Raja mollis* Bigelow & Schroeder, 1950 on the basis of characters other than the clasper structure, since no adult male specimen had been taken. *Malacoraja* was distinguished because of the extraordinary squamation and tail coloration of the type species. Because of similarities in proportional dimensions, tooth count and spination pattern, Hulley (1970) considered *Raja mollis* to be synonymous with *Raja spinacidermis* Barnard, 1923, and later followed Stehmann in the recognition of the subgenus *Malacoraja* to include this species, although no claspers were examined (Hulley 1972*a*).

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The Division of Sea Fisheries, Cape Town, has recently obtained the first adult male specimen of this rare species, during the course of its 1973 Hake Survey Programme, and has donated the specimen to the South African Museum. The specimen not only calls for a description of the anatomy of the clasper and the relevant taxonomic morphology, in an effort to validate the subgenus, but also calls for comment on the phylogenetic position of *Malacoraja*.

MATERIAL

One specimen, an adult male (634,0 mm total length) trawled by R/V *Africana II* at station A 6139 (5 March 1973; 33°43'S 17°21'E; 914 metres; bottom temp. 3,30°C; salinity 34,47‰; O_2 concentration 4,61 ml/litre); in the collection of the South African Museum (SAM–26879). Proportional dimensions according to Hulley (1970) are given in Table 1.

TABLE 1

Raja spinacidermis (SAM–26879). Measurements expressed in mm and as per mileage of the total length.

	mm	‰	*Range* (*Hulley* 1970)
Total length	634,0	—	—
Disc width	450,0	709	660–701
Disc length	335,0	528	515–542
Snout to greatest disc width	198,6	313	307–335
Snout to middle of vent	306,2	483	466–487
Snout to axils of pelvics	272,4	430	—
Middle of vent to 1st dorsal origin	246,3	388	379–417
Snout length	92,6	146	145–166
Preoral length	86,0	136	126–166
Prenasal length	66,5	105	106–136
Eye — horizontal diameter	17,9	28	33–37
Eye + spiracle	23,0	36	42–47
Spiracle	10,8	17	20
Interorbital distance	25,0	39	36–45
Interspiracular distance	41,5	65	64–70
Internasal distance	49,1	77	79–89
Mouth width	57,2	90	83–90
Gill slit lengths: 1st	9,3	15	13–15
3rd	12,0	19	16–17
5th	9,0	14	10–13
Distance between gill slits: 1st	88,2	139	130–147
5th	49,7	78	84–91
1st dorsal fin: height	14,0	22	22–29
base length	28,0	44	47–50
2nd dorsal fin: height	17,6	28	19–27
base length	34,3	54	42–55
Interdorsal space	0	0	0
Teeth (rows in upper jaw)	56		54–60
Vertebral count: Vtr	24		28
Vprd	63		60–65
VΣ	87		88–93

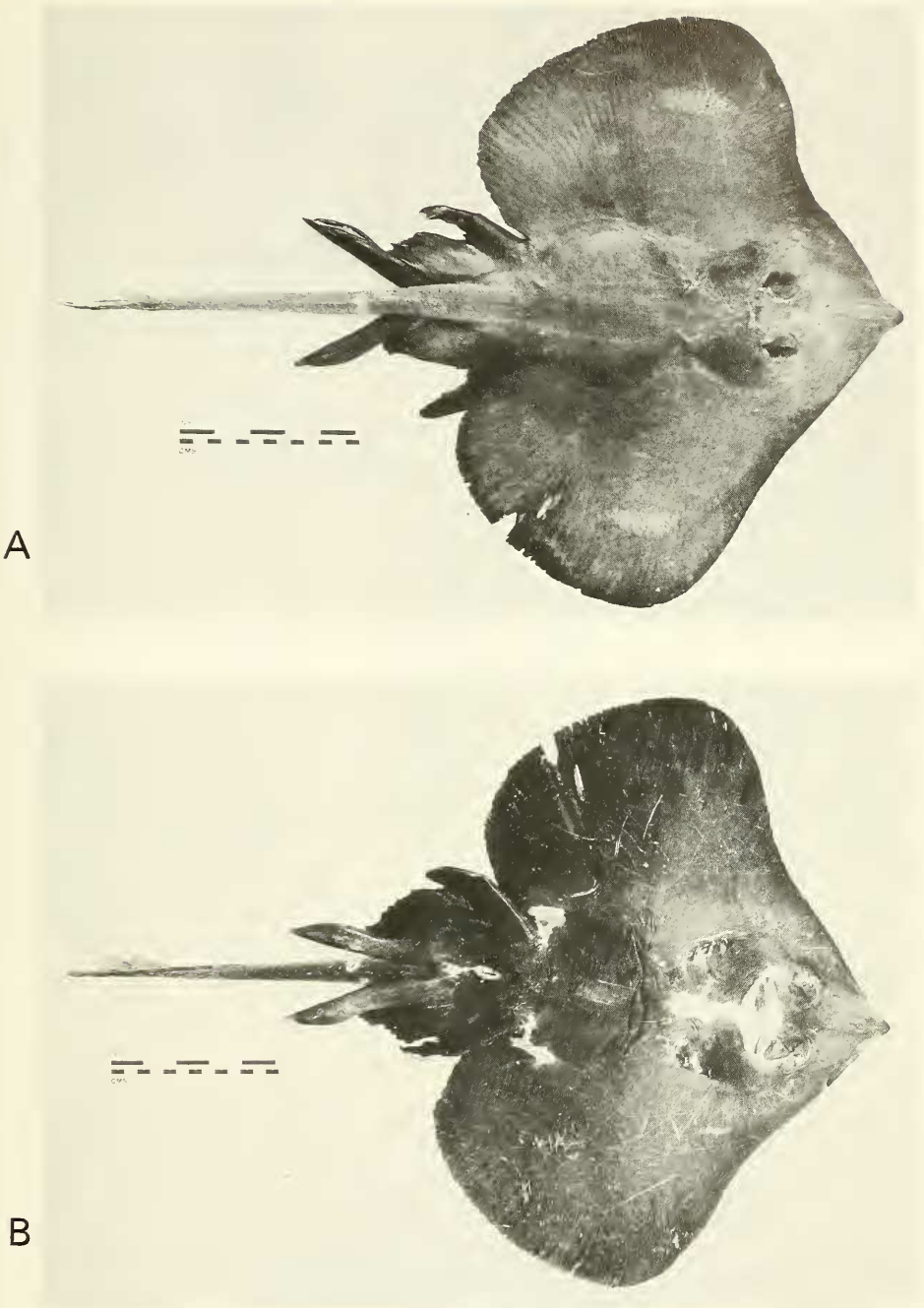

Fig. 1. *Raja* (*Malacoraja*) *spinacidermis*. SAM–26879. A. Dorsal view. B. Ventral view. Scale in cm and in.

MORPHOLOGY (Fig. 1A–B)

The specimen fits the published descriptions of the species and gives some additional information concerning general morphology:

1. Its squamation confirms the original definition of the subgenus, since the upper surface of the disc and tail is completely devoid of thorns and is entirely covered with spinules. A small patch of larger spinules (not typical thorns) is situated in front of the left eye. Malar and alar spines are well developed (Fig. 1A). The ventral surface is naked, except for a small patch of spinules on the tip of the snout, small bands of spinules along the anterior margins of the disc to about half the distance from tip of snout to level of nostrils and the distal half of the tail, which is almost completely covered with spinules.

2. The ventral surface of the disc and tail is uniformly dark brown (Fig. 1B), except for small white areas at the corners of the mouth and between the gill slits, at the axils of the pelvics and at the base of the tail. This coloration does not correspond with the subgeneric and specific diagnostic character of dark ventral tail colour, distinctly marked off from a predominantly white disc, a character based only on juvenile specimens.

3. The teeth of the adult male are in close-set parallel rows, with those in the middle part of the jaws having long, slender, sharply-pointed tips. The teeth of the outer parts of the jaws have low, conical tips.

As far as the ventral coloration is concerned, *Raja spinacidermis* follows a line of development which is well known for most deep-water rays. Juveniles and adolescent specimens bear a few small thorns in the orbital, nuchal and scapular regions and sometimes some enlarged spinules along the midline of the back and tail; the ventral surface of the disc is usually white, with grey or brown markings of varying extent. Thorns on the dorsal surface are almost completely lost in adults, which furthermore show a change in the ventral coloration of the disc to predominantly dark with small white markings in certain areas.

CLASPER STRUCTURE (Figs 2–4)

Claspers moderately long, reaching to about 40 per cent of tail length from axils of pelvics; rather slender, with terminal region barely broadened, distal end pointed and somewhat fimbriate; dorsal and ventral surfaces without dermal denticles; pseudosiphon absent; inner dorsal lobe with longitudinal proximal cleft, upper end of which is covered by a transverse slit; inner ventral lobe with well-developed shield, extending from above level of hypopyle to about four-fifths the length of the glans, with pleated epithelia over most of its surface and with cutting outer edge; insertion of the long rhipidion at level of proximal tip of shield, its distal third fan-shaped and with porous surface; sentinel well developed and slightly S-shaped, covered with fleshy

integument; spike blunt and hardly projecting from midline of clasper, placed below tip of sentinel; dike well developed along midline of distal half of glans, rising in 90° angle from inner edge of shield and covered with thin integument; medium-sized funnel below distal end of dike, formed as obtuse tip covered

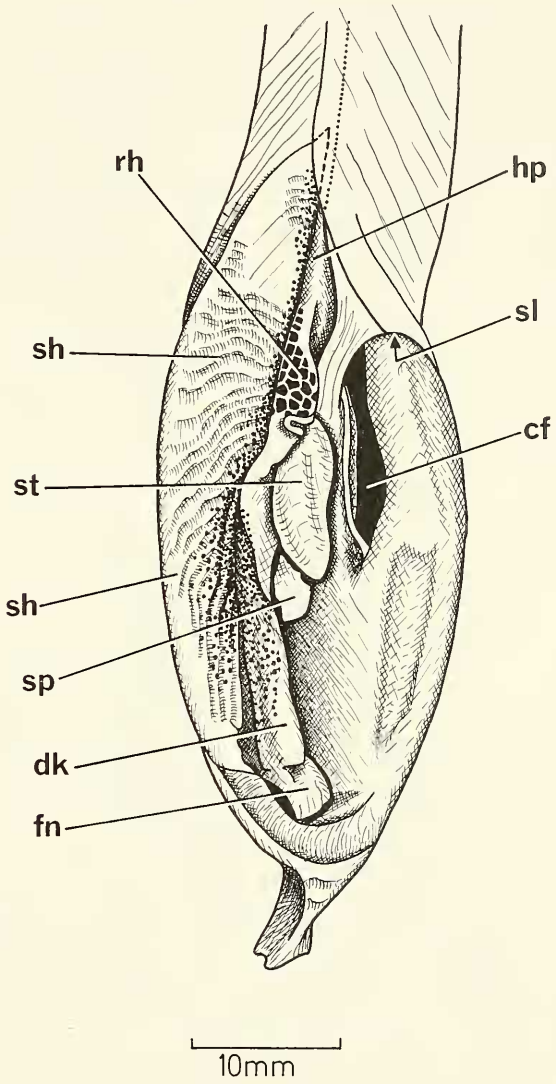

Fig. 2. *Raja* (*Malacoraja*) *spinacidermis*. Lateral view of left clasper, opened to show structural features of the glans.

cf—cleft; dk—dike; fn—funnel; hp—hypopyle; rh—rhipidion; sh—shield; sl—slit; sp—spike; st—sentinel

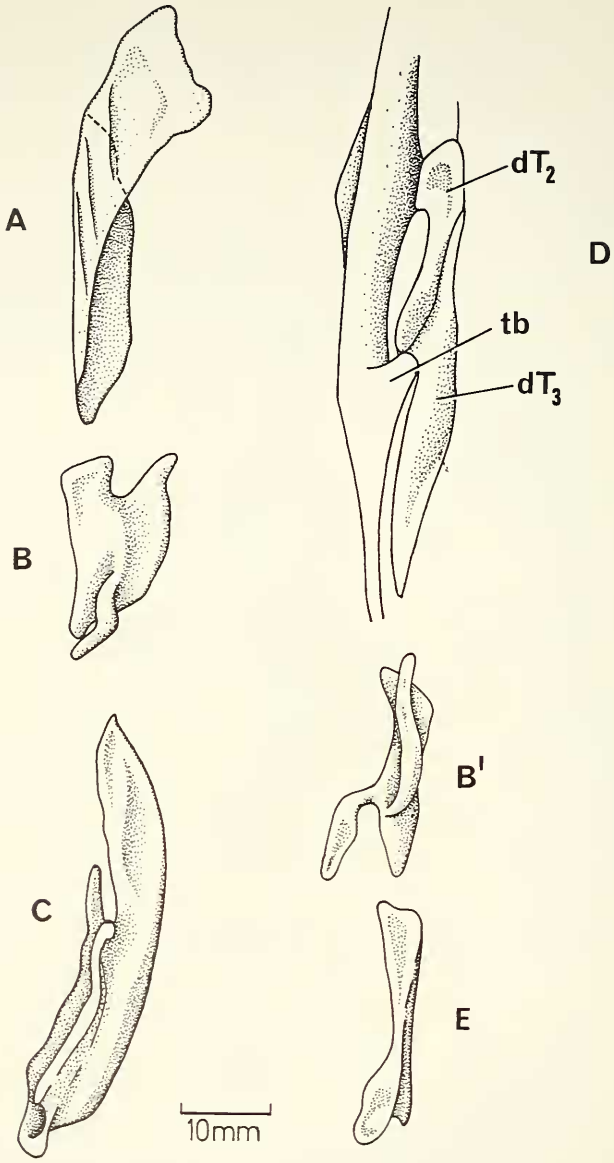

Fig. 3. *Raja* (*Malacoraja*) *spinacidermis*. Cartilages of the terminal group of the right clasper. A. Dorsal terminal 1 (dorsal view). B. Accessory terminal 1 (dorsal view). B′. Accessory terminal 1 (lateral view). C. Ventral terminal (dorsal view). D. Dorsal terminal 2 and dorsal terminal 3 (dorsal view). E. Accessory terminal 2 (dorsal view).

dT_2—dorsal terminal 2; dT_3—dorsal terminal 3; tb—terminal bridge.

with fleshy integument. Entire inner edge of shield darkly pigmented to level of proximal end of dike, becoming diffuse laterally and distally on shield and distally on dike.

Axial cartilage slender distally, but with slightly spatulate tip; dorsal marginal with short distal extension, ventral marginal arched; dorsal terminal 1 cartilage large, twisted and connected distally with distal tip of ventral terminal cartilage, without shelf for insertion of *M. dilatator*, but with 3 longitudinal

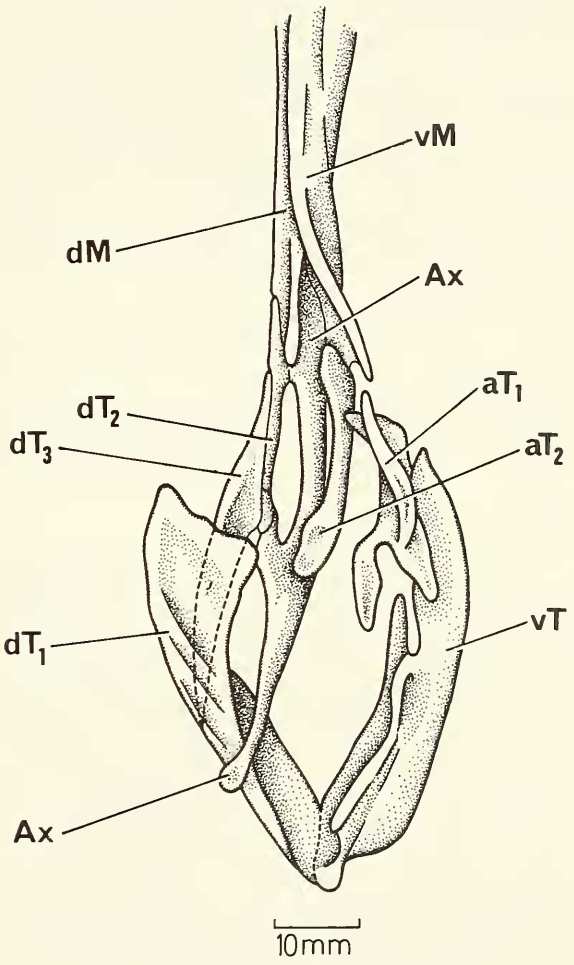

Fig. 4. *Raja* (*Malacoraja*) *spinacidermis*. Cartilages of right clasper (exploded).
Ax—axial; aT_1—accessory terminal 1; aT_2—accessory terminal 2; dM—dorsal marginal; dT_1—dorsal terminal 1; dT_2—dorsal terminal 2; dT_3—dorsal terminal 3; vM—ventral marginal; vT—ventral terminal.

ridges; dorsal terminal 2 and 3 cartilages simple, forming framework of dorsal lobe, with dT_2 and dT_3 making contact with a well-developed terminal bridge, which is an offshoot of the Ax; dT_2 and Ax bordering proximal cleft; ventral terminal cartilage large, with outer lateral margin forming the shield, with dorsal crest the dike, with distal tip the funnel, and with anterior notch linked with aT_1; accessory terminal 1 cartilage somewhat U-shaped proximally and with well-developed lateral projection forming the sentinel; accessory terminal 2 simple, with spatulate distal extremity, closely attached to the Ax proximally and distally, but free medially.

With regard to the external components of the glans, *Malacoraja* is characterized by:

(i) very few structures on the inner dorsal lobe, but particularly a single, deep, proximal cleft combined with a transverse slit,
(ii) a very long, prominent shield, covered with laminate epithelia and combined with a dike and funnel at its distal end,
(iii) a sentinel and spike located rather far proximally in the glans,
(iv) a medium-sized rhipidion and the absence of a pseudosiphon.

Diagnostic characters of the clasper skeleton include:

(i) the extraordinary shape of the aT_1 cartilage, which is unparalleled among investigated *Raja* species,
(ii) the terminal bridge is neither formed by separate cartilages nor by dT cartilages attached directly to the Ax, but is a massive offshoot of the Ax itself.

NEUROCRANIUM (Fig. 5)

Neurocranium typically guitar-shaped and markedly constricted across the orbital region, with well-developed post-orbital processes, short otic region, and moderately-developed jugal arches; nasal capsules massive and directed obliquely forward to about 55° to median axis, with ethmoidal nerve foramen at leading edge; maximum width 60,6 per cent of total length of skull; rostral cartilage projecting from cranium to tip of snout as strong but tapering rod, without a segment; length of rostrum 53,8 per cent of total length of skull; rostral appendices fused throughout their entire length to rostral bar and extending posteriorly slightly more than two-thirds the distance from tip of snout to level of anterior fontanelle or extend backward 60,6 per cent of length of rostrum: radial cartilages of pectoral fin extending anteriorly, but falling well short of tip of snout; anterior fontanelle extending forward to 15,5 per cent of the length of rostrum, without anterior grooving and separated from posterior fontanelle by narrow epiphysial bridge; orbito-nasal canal foramen comparatively small, optic foramen situated well forward: anterior cerebral vein foramen well above level of optic foramen and situated close to internal foramen of ophthalmic nerve; external foramen of ophthalmic nerve large and positioned comparatively more posteriorly, at about level of antorbital processes.

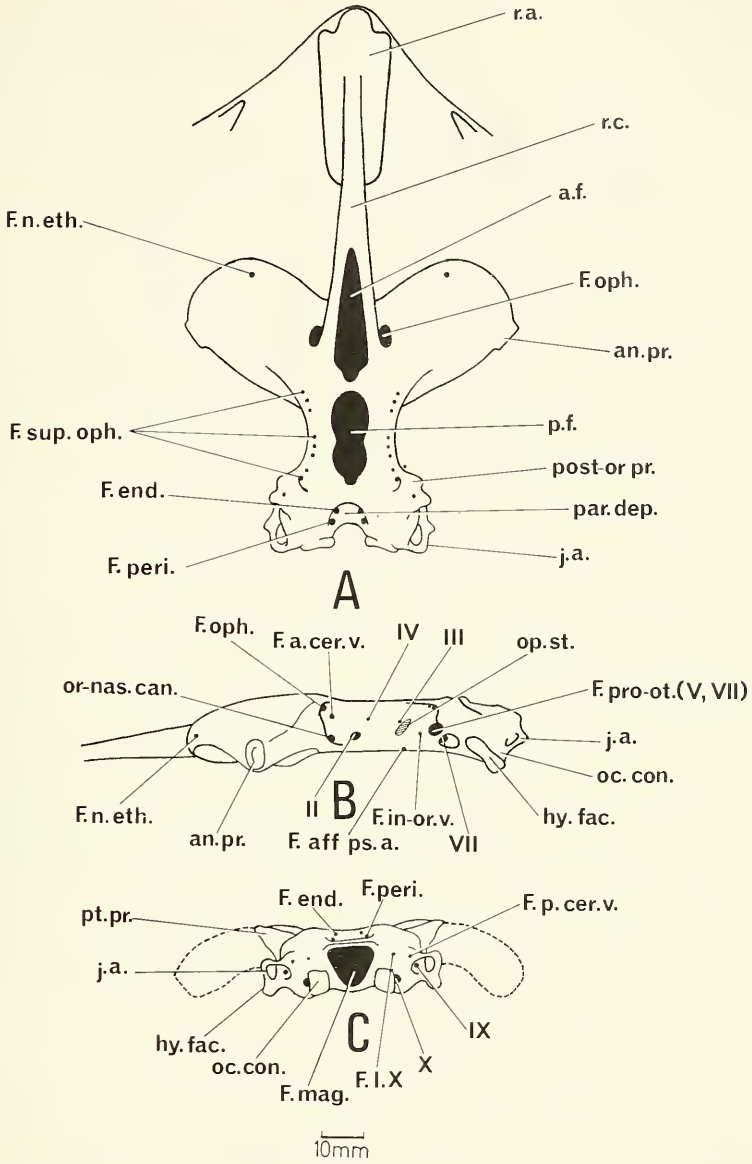

Fig. 5. *Raja* (*Malacoraja*) *spinacidermis*. Neurocranium. A. dorsal view. B. lateral view. C. posterior view.

a.f.—anterior fontanelle; an.pr.—antorbital process; F.a.cer.v.—anterior cerebral vein foramen; F.aff.ps.a.—afferent pseudobranchial artery foramen; F.end.—endolymphatic foramen; F.in-or.v.—interorbital vein foramen; F.l.X—foramen of lateralis branch (X); F.mag.—foramen magnum; F.n.eth.—ethmoidal nerve foramen; F.oph.—ophthalmic foramen; F.p.cer.v.—posterior cerebral vein foramen; F.peri.—perilymphatic foramen; F.pro-ot.—pro-otic foramen; F.sup.oph.—superficial ophthalmic foramen; hy.fac.—hyomandibular facet; j.a.—jugal arch; oc.con.—occipital condyle; or-nas.can.—oro-nasal canal; op.st.—optic stalk; p.f.—posterior fontanelle; par.dep.—parietal depression; post-or.pr.—postorbital process; pt.pr.—pterotic process; r.a.—rostral appendix; r.c.—rostral cartilage; II—optic nerve foramen; III—oculomotor nerve foramen; IV—pathetic (trochlear) nerve foramen; VII—foramen of hyomandibular branch (VII); IX—glossopharyngeal nerve foramen; X—vagus nerve foramen.

Diagnostic characters are:

(i) an anterior fontanelle clearly marked off on all sides,
(ii) a rostral cartilage longer than the neurocranium,
(iii) the maximum width of the skull more than 50 per cent of its total length,
(iv) the rostral appendices more than half the length of the rostral bar, fused with the latter over their entire length.

DISCUSSION

There is no doubt that the spination pattern of the disc and tail and the complete absence of large thorns along the midline of the back and tail is unique in *Raja spinacidermis*. The coverage of the dorsal surface by close-set spinules is a character shared by species of *Breviraja* (*B. stehmanni* off South Africa), of *Bathyraja* (*B. smithii* off South Africa) (Hulley 1972*a*, 1972*b*), and rarely of *Raja* (e.g. *R. senta* in the north-western Atlantic), but these species either have specialized snout conditions and/or possess at least midline thorns on the dorsal surface. While the enormous size of the nasal capsules appears to be correlated mainly with depth distribution, e.g. *Raja radiata* and *R. robertsi* (Hulley 1972*a*), the length of the rostral cartilage and especially its appendices, is rather extraordinary among short-snouted *Raja* species. Both the rostral cartilage and the appendices are typically rajid in form, but their characteristics can be interpreted as an ancestral condition, which approximates *Dipturus* and single species of other subgenera, e.g. *Raja fullonica* (Stehmann 1970: 146, pl. 22).

The anatomy of the clasper of *Raja spinacidermis* shows a number of similarities to that of *Breviraja*-species (Hulley 1972*b*; Stehmann 1976): the position and general form of the sentinel and spike (aT_1 and aT_2); the arrangement of the dT_2 and dT_3 and their connection with a well-developed terminal bridge; and the form of the vT, which distally is firmly bonded to the tip of the dT_1. The form of the aT_1 cartilage in *Raja spinacidermis* is unique among *Raja*-species that have thus far been investigated. The form of the dT_1, the association of dT_2, dT_3 and the terminal bridge, the form of the vT (resulting among others in the formation of a prominent shield), and the lack of an external pseudosiphon, point to a closer association with species of the subgenus *Dipturus* (Hulley 1972*a*). *Malacoraja* also shows a relation to *Amblyraja*, *Leucoraja* and *Rajella* in the general form of the dT_1 and vT, especially in the position of the anterior notch of the latter (Hulley 1972*a*: 38), and furthermore in the bonding of the distal extremities of both these cartilages (cf. Stehmann 1970, pls 11–12).

In summary then, *Malacoraja* is also confirmed as a separate and valid subgenus of *Raja* by conditions of clasper and skull, which are the most important characters in modern rajid taxonomy. It possesses a true rajid condition of the clasper and skull, but shows characteristics in both, which are intermediate between *Dipturus* and *Breviraja*-species. It may therefore be interpreted as the subgenus linking the genera *Breviraja* and *Raja*. With regard to *Raja*, *Malacoraja* is closely associated to the evolutionary line of the subgenera

Dipturus/*Rajella*/*Amblyraja*/*Leucoraja*. A strict application of Vprd values would indicate a common ancestry for *Malacoraja* and *Breviraja* rather than a direct lineage and would point to an origin from some ancestral *Dipturus*-species. Further, the depth distribution pattern in *Malacoraja* would support the hypothesis that *Breviraja*-species represent an early split from the rajid condition, which penetrated abyssal regions, but which retained the neotenous condition of the snout as an increased advantage in grubbing.

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